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PENSOFT

Checklist of the Myriapoda in Cretaceous Burmese amber and a correction of the Myriapoda identified by Zhang (2017)

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Abstract

An inventory of the Myriapoda (Diplopoda, Chilopoda, Symphyla) from Cretaceous Burmese amber, Myanmar, is presented, including the oldest and/or first fossil record for numerous orders. For millipedes (Diplopoda) 527 records, including 460 new specimens determined by us, belonging to 13 of 16 recent orders are listed: Polyxenida, Glomeridesmida, Glomerida, Siphonophorida, Polyzoniida, Platydesmida, Siphoniulida, Chordeumatida, Polydesmida, Stemmiulida, Callipodida, Spirostreptida and Spirobolida. For centipedes, 33 records for 4 of the 5 recent orders are listed: Scutigeromorpha, Lithobiomorpha, Scolopendromorpha and Geophilomorpha. For Symphyla, three records for both families, Scutigerellidae and Scolopendrellidae, are listed. The majority of Diplopoda records (30.5%) are Polydesmida. The record of the Polyzoniida includes first instar octopod juveniles. The checklist includes the first fossil representatives known of the Platydesmida, as well as the oldest known fossils of the Polyxenida, Glomeridesmida, Glomerida, Siphonophorida, Polyzoniida, Siphoniulida, Spirostreptida, as well as both Symphyla families. Misidentifications by Zhang (2017) are corrected; while most Chilopoda in that list are correct, almost all Diplopoda are misidentified.

Key words

Cretaceous; Myanmar; Fossil; Diplopoda; Chilopoda; Symphyla.

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Introduction

Burmese amber from the Hukawng Valley in northern Myanmar dates back to the Albian-Cenomanian boundary (Cretaceous), ca 99 mya (Shi et al. 2012). For a review on the history and geology of Burmese amber see Zherikhin and Ross (2000), Grimaldi et al. (2002), and Cruickshank and Ko (2003). Since the 1990s Burmese amber has yielded many important fossils. Thus many spectacular arthropod fossils were described, such as the extinct insect order Alienoptera (Bai et al. 2016). A checklist of arthropod taxa recorded from Burmese amber was compiled by Ross et al. (2010) and is regularly updated online (Ross 2018), currently comprising 1013 species, of which 941 species belong to the Arthropoda. Myriapoda are mainly soil animals (David 2015) and contain 4 classes: Diplopoda (millipedes), Chilopoda (centipedes), Pauropoda and Symphyla, altogether containing ca 18,000 described extant species (Bonato and Zapparoli 2011, Scheller 2011, Szucsich and Scheller 2011, Enghoff et al. 2015). The Myriapoda have an old (> 400 my) but also very fragmentary fossil record (see Shear and Edgecombe 2010, Edgecombe 2015), including the oldest known terrestrial animal (Wilson and Anderson 2004). From

Burmese amber Ross (2018) listed 21 records of Myriapoda, of which 5 species were described: 3 Diplopoda (Cockerell 1917, Liu et al. 2017a), 1 Chilopoda (Bonato et al. 2014), and 1 Symphyla (Moritz and Wesener 2018). Burmese amber yielded the oldest fossil of the class Symphyla, the first known fossil representative of the family Scolopendrellidae (Moritz and Wesener 2018), and the first known fossils of the millipede order Siphoniulida (Liu et al. 2017a).

The opportunity to study several hundreds of Myriapoda inclusion from 4 private collections in Germany resulted in the discovery of numerous new records, which are presented here. These new records include the oldest known fossils of the millipede orders Glomeridesmida, Glomerida, both Siphonophorida families, Polyzoniida, Platydesmida, Stemmiulida and Spirostreptida. Unfortunately, the vast majority of specimens are in the hands of private collectors, and it can only be hoped that they will be made accessible to the general scientific community in the near future.

Methods

Abbreviations:

NHML Natural History Museum of London, UK
NMS National Museums Scotland, Edinburgh, UK
In. Prefixed registration number at the NHML (Rasnitsyn and Ross 2000)
AMNH American Museum of Natural History, New York, USA
BuB Private collection of Patrick Müller, Käshofen, Germany
Wu Private collection of Jörg Wunderlich, Hirschberg, Germany
CG Private collection of Carsten Gröhn, Glinde, Germany
RO Private collection of Rainer Ohlhoff, Saarbrücken, Germany
ZFMK Zoological Research Museum Alexander Koenig, Bonn, Germany

Data from two Museum collections (NHML, AMNH) are compiled from the literature, while specimens deposited in the ZFMK were observed. Literature references without any picture or source of the amber or specimens are not included in this list (e.g. specimens mentioned in conference abstracts, or online lists without any voucher information). In addition specimens, often fragmented, that cannot be securely determined to order level, are not included. Specimens belonging to 4 private collections, containing the majority of the records, were examined and determined to order, in some cases also family level. These examined collections include a total of 480 specimens.

All examined specimens are from the Noije Bum amber mine in the Hukawng Valley, Kachin State, Northern Myanmar (26°15′ N, 096°34′ E). All necessary permits are present and available upon request.

Determinations and classifications follow the characters given in the recent literature (Bonato and Zapparoli 2011, Szucsich and Scheller 2011, Blanke and Wesener 2014, Enghoff et al. 2015). In our list numbers in parentheses refer to the total number of specimens per taxonomic group; M = male, F = female, ? = sex unknown.

As many Diplopoda families can only be securely determined by studying the male copulatory legs (gonopods or telopods), which is beyond the scope of this list, such determinations were not undertaken in the Glomerida, Polydesmida, Callipodida, Stemmiulida, Spirostreptida and Spirobolida, even if the outer appearance of the fossils might be similar to extant species, because convergent evolution cannot be ruled out, and extinct representatives could resemble morphotypes of extant but different families.

Microphotographs were obtained using a Canon EOS 7D camera equipped with a magnifier lens. Image stacking was performed in Zerene Systems Stacker (Version 1.04).

Results

Class DIPLOPODA deBlainville in Gervais, 1844

Order Polyxenida Verhoeff, 1934

Family undetermined (5)

New records. 1 ?, BuB2658; 1 ?, BuB2659; 1 ?, BuB2984; 1 ?, BuB3028; 1 ?, RO my295.

Identification. Members of the order Polyxenida are among the easiest Diplopoda to identify. They are the only soft-bodied millipedes whose body is covered by tufts of hair and which carry caudal bundles of trichomes (Enghoff et al. 2015).

Family Polyxenidae Lucas, 1840 (8)

New records. 1 ?, BuB634; 1 ?, BuB2612; 1 ?, BuB2961; 1 ?, BuB2966; 1 ?, Wu F3358/Bu/CJW; 1 ?, Wu F3384/Bu/CJW; 1 ?, Wu F3389/Bu/CJW; 1 ?, Wu F3394/Bu/CJW.

Identification. These 8 specimens were thankfully determined to the family level by the taxonomic expert of the group, Megan Short, based on photographs (see Acknowledgements). The diagnostic characters include: presence of 10 tergites, 13 pairs of legs, as well as a special arrangement of hairs.

Family Synxenidae Silvestri, 1923 (68)

Literature records. 3 ?, AMNH (Grimaldi et al. 2002); NHML: 4 ?, In.19102-3; 6 ?, In.19104-6; 2 ? In.19177-22; 24 ?, In.19123; 5 ?, In.20149; 18 In.20150; 1 ?, In.20169 (Rasnitsyn and Ross 2000); 1 ?, (Zhang 2017: 146); 1 ?, NMS G.2010.41.41 (Ross and Sheridan 2013).

***Phryssonotus burmiticus* (Cockerell, 1917)**

Cockerell 1917, Rasnitsyn and Golovatch 2004, Zhang 2017.

New records. 1 ?, Wu F3388/Bu/CJW; 1 ?, RO my107; 1 ?, RO my191.

Order Glomeridesmida Latzel, 1884

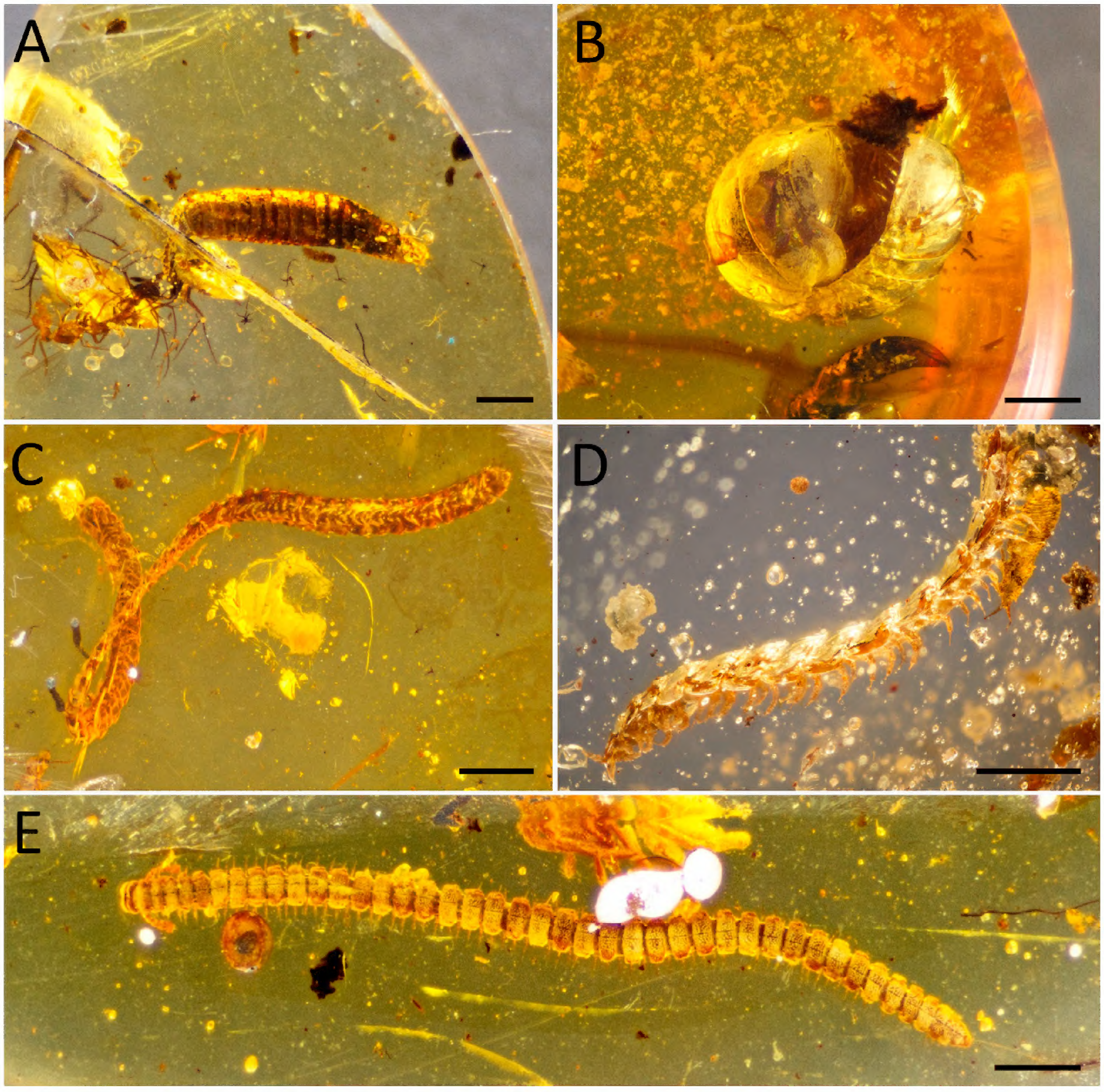

Figure 1. Pentazonia and Colobognatha in Burmese amber, microphotographs. **A.** Glomeridesmida (BuB2413), dorsal view. **B.** Glomerida (BuB2603) lateral view. **C.** Siphonophorida (BuB823), ventral view. **D.** Polyzoniida (BuB979) lateral view. **E.** Platydesmida (BuB2670), dorsal view. Scale bars = 1 mm.

Family Glomeridesmidae Latzel, 1884 (3)

New records. 1 M, ZFMK MYR06117; 1 M, BuB2423; 1 ?, BuB3285.

Figure 1A

Identification. Members of the Glomeridesmida, family Glomeridesmidae can be easily identified by the following head characteristics: the absence of ommatidia, a large Tömösváry organ which is circular. Furthermore, their body consists of 19 tergites plus anal shield (Enghoff et al. 2015). The determination can be further confirmed by the presence of well-developed and visible telopods as 2 of the specimens are males. The specimens also fit in all characters to the recent members of the family Glomeridesmidae; the only other family of the Glomeridesmida, Termitodesmidae, is morphologically strongly derived (Enghoff et al. 2015).

Order Glomerida Leach, 1814

Family undetermined (37)

New records. 1 M, CG-My7276; 1 ?, CG-BURMA11119; 1 ?, CG-BURMA11127; 3 ?, BuB992; 3 ?, BuB1821; 1 ?, BuB2438; 1 ?, BuB2603; 1 ?, BuB2604; 1 ?, BuB2703; 3 ?, BuB2704; 1 ?, BuB2705; 1 ?, BuB2706; 1 ?, BuB2707; 1 ?, BuB2718; 1 ?, BuB2957; 1 ?, BuB2990; 1 ?, BuB2995; 1 ?, BuB2996; 1 ?, BuB3013; 1 ?, BuB 3014; 1 ?, BuB3015; 1 ?, BuB3016; 1 ?, BuB3053; 1 ?, BuB3058; 1 F, BuB3257; 1 ?, BuB3259; 1 ?, ZFMK MYR06116; 1 ?, ZFMK MYR07365; 1 ?, ZFMK MYR07371; 1 ?, ZFMK MYR07372; 1 ?, ZFMK MYR07376.

Figure 1B

Identification. All these pill millipede specimens were determined as members of the Glomerida based on the characteristic head characters of the order. Glomerida can

be distinguished from the Sphaerotheriida by the shape of the Tömösváry organ, the insertion point of the antenna and many other characteristics (Oeyen and Wesener 2018). The family classification of the Glomerida is based on the telopods, which currently prevents any more detailed determinations.

Order Siphonophorida Newport, 1844

Family undetermined (25)

New records. 1 F, BuB823; 1 M, BuB977; 1 ?, BuB982; 1 M, BuB905; 1 F, BuB1835; 1 F, BuB1951; 1 M, BuB1959; 1 ?; Bub1966b; 1 ?, BuB1970; 1 F, BuB1971; 1 F, BuB1977; 1 F, BuB1978; 1 F, BuB1980, 1 M, BuB1981; 1 M, BuB1991; 1 ?, BuB2605; 1 ?, BuB2973; 1 F, BuB3019; 1 M, BuB3035; 1 M, BuB3036; 1 ?, BuB3037; 1 ?, BuB343; 1 F, BuB3045; 1 F, BuB3054; 1 ?, BuB3057.

Figure 1C

Identification. Members of the order Siphonophorida can be easily identified based on the beak-like projection of the head, the absence of eyes, as well as the absence of a dorsal suture (Enghoff et al. 2015). The trunk is usually very slender with a length/width ratio of 1/10 or more.

Family Siphonophoridae Newport, 1844 (35)

Literature record. 4 ?, AMNH (Grimaldi et al. 2002).

New records. 1 F, RO my130; 1 ?, RO my330; 1 F, BuB1030; 1 F, BuB2243; 1 F (broken), BuB644; 1 ? (broken), BuB73; 1 ?, BuB828; 1 F, BuB978; 1 F, BuB981; 1 ?, BuB984; 1 ?, BuB986; 1 F, BuB1143; 1 F, BuB1159; 1 F, BuB2963; 1 F, BuB2973; 1 ?, BuB2986;1 M, BuB2989; 1 ?, BuB2997; 1 M, BuB3006; 1 M, BuB3007; 1 ?, BuB3010; 1 M, BuB3034; 1 ?, BuB3047; 1 F, BuB3052;1 F, BuB3239; 1 ?, BuB3245; 2 F, BuB3261; 1 F, BuB3262; 1 ?, Wu F3149/Bu/CJW; 1 ?, Wu F3393/Bu/CJW.

Identification. Members of the family Siphonophoridae can be easily identified based on the head characteristics (Enghoff et al. 2015): the antennae is straight, with large sensory pits on the antennomeres 5 and 6. The antennomere 2 is as long as the others.

Family Siphonorhinidae Cook, 1895 (12)

New records. 1 M, BuB1086; 1 M, BuB997; 1 F, BuB1123; 1 F, BuB1150; 1 F, BuB1822; 1 F, BuB1838; 1 F, BuB1842; 1 F, BuB1845; 1 ?, BuB1851; 1 ?, BuB2979; 1 F, BuB3243; 1 ?, BuB3283.

Identification. Members of the order Siphonorhinidae can be easily identified based on the head characteristics (Enghoff et al. 2015): the antennae is elbowed, the antennomere 2 is twice as long as antennomere 3, lacking any large sensory pits.

Order Polyzoniida Gervais, 1844

Family undetermined (35)

New records. 1 F, BuB112; 1 F, BuB219; 1 F, BuB913; 8 F, BuB914; 1 F, BuB919; 1 ?, BuB1031-B; 1 ?, BuB1994; 1 ?, BuB1996; 1 F, BuB2964; 1 ?, BuB2965; 1 F, BuB2980; 1 ?, BuB3017; 1 ?, BuB3033; 1 ?, BuB3044; 3 ?, Wu F3167/BU/CJW; 1 ?, Wu F3172/BU/CJW; 1 ?, Wu F3201/Bu/CJW; 1 ?, Wu F3202/Bu/CJW; 1 ?, Wu F3107/Bu/CJW; 1 F, Wu F3390/Bu/CJW; 1 ?, Wu F3395/Bu/CJW; 1 ?, Wu F3400/Bu/CJW; 1 F, Wu F3401/Bu/CJW; 1 F, RO my153; 1 F, RO my199.

Identification. Members of the order Polyzoniida are flat, wide, with a width/length ratio of 1/10 to 1/3. The head is characteristically elongated into a well-rounded snout, with 2+2 to 4+4 ommatidia. The tergites lack a dorsal suture (Enghoff et al. 2015).

Family Siphonotidae Cook, 1895 (67)

New records. 1 ?, BuB612; 1 F, BuB825; 1 F, BuB837; 1 F, BuB817; 1 F, BuB824; 1 F, BuB831; 1 F, BuB826;; 1 F, BuB836; 1 F, BuB840; 1 F, BuB925; 1 F, BuB979; 1 F, BuB1130; 1 F, BuB1034; 1 F, BuB1087;1 F, BuB1161; 3 ?, BuB1162; 1 F, BuB1163; 1 F, BuB1164; 1 F, BuB1166; 1 F, BuB1167; 1 F, BuB1834; 2 F, BuB1837; 1 F, BuB1853; 1 F, BuB1854; 1 F, BuB1855; 2 F, BuB1856; 1 F, BuB1956; 1 F, BuB1966; 1 F, BuB1972; 1 F, BuB1976; 1 F, BuB1983; 2 ?, BuB1984; 1 F, BuB1993; 1 F, BuB2607; 1 F, BuB2608; 1 F, BuB2609; 1 F, BuB2610; 1 F, BuB2611; 1 ?, BuB2615; 1 ?, BuB2656; 1 ?, BuB2657; 1 F, BuB3266; 1 F, BuB3268; 1 F, BUB3270; 2 F, BuB3272; 1 F; BuB3273; 1 juv., BuB3280; 5 F, BuB3281; 5 F, BuB3284; 1 F, ZFMK MYR06122; 1 F, ZFMK MYR06124; 1 F, ZFMK MYR07374; 1 F, ZFMK MYR07381.

Figure 1D

Identification. Members of the Siphonotidae have the following characters (Enghoff et al. 2015): the posterior tergal margins is "normal", not upturned. The telson is surrounding the anal valves in ventral view. The head is free, not covered by the first tergite. The leg claws carry a paronychium.

Order Platydesmida de Saussure, 1860

Family Andrognathidae Cope, 1869 (8)

New records. 1 M, Wu F3391/Bu/CJW; 1 F, BuB1413; 1 M, BuB2670; 1 M, BuB2991; 1 M, BuB3237; 1 F, BuB3291; 1 M, BuB3307; 1 F, BuB3308.

Figure 1E

Identification. Members of the order Platydesmida are morphologically variable, the head is only weakly elongated, lacking eyes. The tergites and pleurites are fused, but have dorsally a clearly evident suture (Blanke and Wesener 2014).

Order Siphoniulida Pocock, 1894

Family Siphoniulidae Pocock, 1894 (2)

***Siphoniulus muelleri* Liu, Rühr & Wesener, 2017**

Literature record. 1 F, ZFMK MYR6098 (Liu et al. 2017a).

***Siphoniulus preciosus* Liu, Rühr & Wesener, 2017**

Literature record. 1 F, ZFMK MYR5543 (Liu et al. 2017 a).

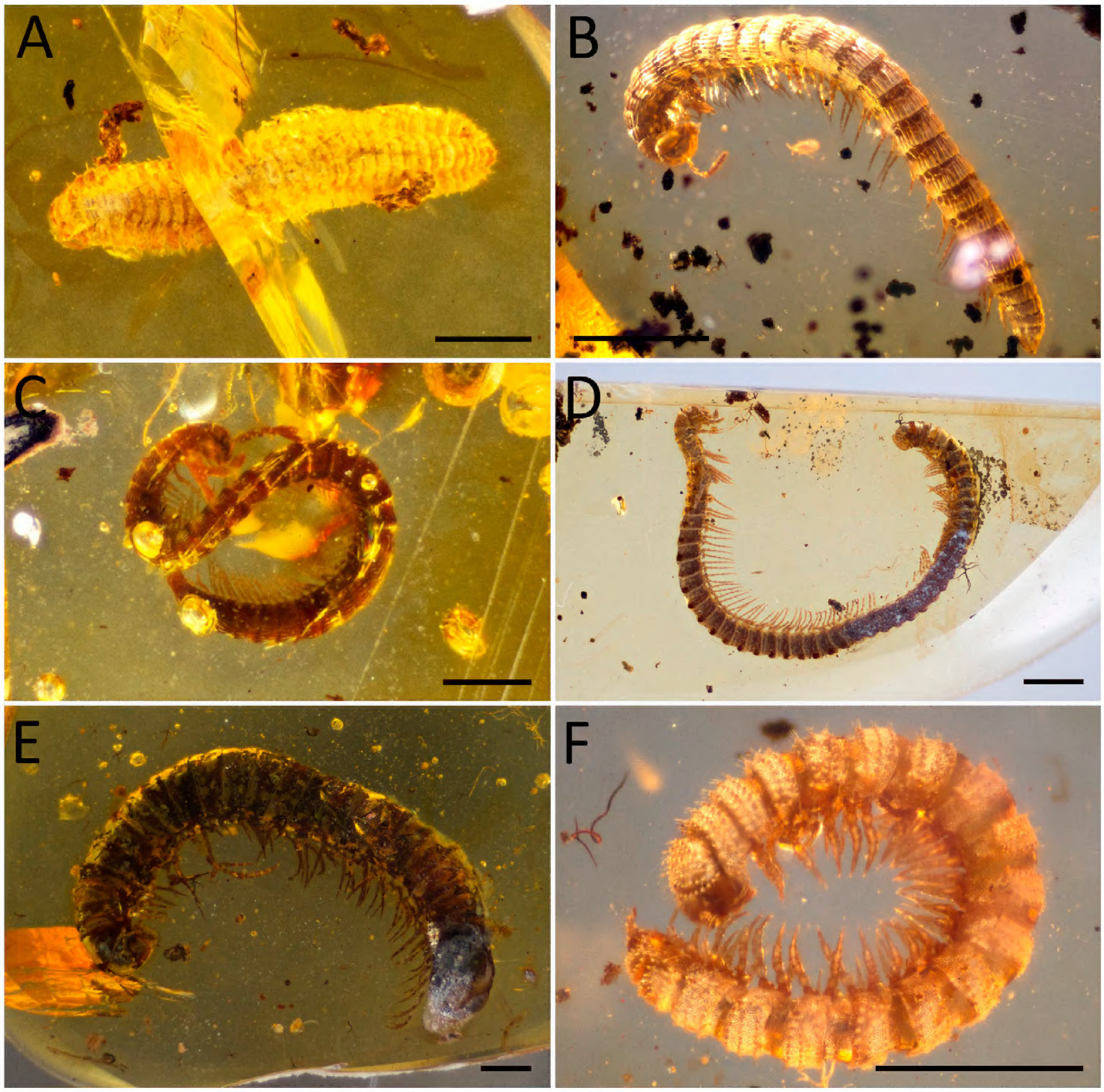

Figure 2. Nematophora, Juliformia and Polydesmida in Burmese amber. **A.** Chordeumatida: Heterochordeumatidae (BuB642), dorsal view. **B.** Stemmiulida (BuB907), lateral view. **C.** Callipodida (BuB1976-B), lateral view. **D.** Spirostreptida: Cambalidea (BuB1151), lateral view. **E.** Spirobolida (BuB1145), lateral view. **F.** Polydesmida (BuB1031-A), lateral view. Scale bars = 1 mm.

Order Chordeumatida Pocock, 1894

Family undetermined (3)

New records. 1 ?, BuB0974; 1 ?, BuB1978; 1 M, BuB2978.

Identification. Chordeumatida can be identified based on the presence of 25–31 tergites with a dorsal suture, an anal segment carrying 4 spinnerets, and tergites with 3+3 characteristic macrosetae (Enghoff et al. 2015). The order has many recent families, which in most cases can only be identified based on a careful examinations of the male copulatory legs.

Family Heterochordeumatidae Pocock, 1894 (20)

New records. 1 F,Wu F2806/Bu/CJW; 1 F, BuB0642; 2 M, BuB0833; 1 F, BuB0899; 1 M, BuB1141; 1 F, BuB1410; 1 F, BuB1411; 1F, BuB1412; 1 M, BuB1823; 1 ?, BuB1827; 1 M, BuB2685; 1 F, BuB3022; 1 ?, BuB3030; 1 F, BuB3051; 1 ?, BuB3056; 1 M, ZFMK MYR05545; 1 M, ZFMK MYR06123; 1 M, ZFMK MYR06624; 1 M, ZFMK MYR07367.

Figure 2A

Identification. Species of the family Heterochordeumatidae are among the most unusual Chordeumatida, with wide paranota resembling some species of Platydesmida (which also share the dorsal suture) and Polydesmida. The collum partly conceals the head.

Order Stemmiulida Pocock, 1894

Family undetermined (8)

New records. 1 M, BuB994; 1 F, BuB1961; 1 ?, BuB1968; 1 ?, BuB2998; 1 ?, BuB3009; 1 F, BuB3038; 1 ?, BuB3241; 1 M, ZFMK MYR07378.

Figure 2B

Identification. Members of the Stemmiulida have a very characteristic appearance. The body is cylindrical, carrying spinnerets at the telson. The head has laterally 1–3 large ommatidia. The order has only 1 recent family (Enghoff et al. 2015), but we hesitate to place these fossils in the recent family without a more detailed morphological investigation.

Order Callipodida Pocock, 1894

Family undetermined (1)

New record. 1 F, ZFMK MYR07366.

Figure 2C

Identification. Members of the order Callipodida have a characteristic habitus, the head has numerous ommatidia, the segments are cylindrical, with free sternites, lacking a dorsal suture. The telson is carrying spinnerets. The surface is often with characteristic crests (like in numerous Spirostreptida and Cambalidea, which, however, lack free sternites and spinnerets). The telson has divided anal valves (paraprocts), a unique character (Enghoff et al. 2015). The female vulva often extended into an elongated ovipositor, which is sometimes heavily modified resembling a clasping organ in recent species. The extended ovipositor is clearly visible in our single female specimen.

Order Spirostreptida Brandt, 1833

Suborder Cambalidea Cook, 1895

Family undetermined (19)

New records. 1?, BuB1115; 1?, BuB1144; 1 F, BuB1165; 1?, BuB1824; 1 F, BuB1825; 1 F, BuB1826; 1 F, BuB1990; 1 F, BuB1955; 1 M, BuB1962; 1?, BuB2981; 1?, BuB3005; 1?. BuB3012; 1?, BuB3250; 1 M, BuB3255; 1 M, ZFMK MYR06121; 1 M, ZFMK MYR07368; 1 M, ZFMK MYR07369; 2 F, ZFMK MYR07370.

Figure 2D

Identification. The tergites, pleurites and sternites are completely fused into body rings. The head is lacking a median suture. The anterior legs have a characteristic gap between leg 3 and 4, as legs 4 and 5 are on the posterior end of body ring 5. The specimens listed here are a bit unusual as they have frontal setae on their head, a character absent in all recent Spirostreptida. The presence of 2 pairs of gonopods in the males identify those specimens as members of the suborder Cambalidea, as species belonging to the other suborder, Spirostreptidea, only have one pair of gonopods (Enghoff et al. 2015).

Family Cambalidae Bollman, 1893 (1)

New record. 1 M, ZFMK MYR06696.

Identification. This 1 specimen among the numerous samples of Spirostreptida differs from the others in the absence of frontal setae on the head, in being more similar to recent Cambalidea. The specimen has the gonopods visible, showing anterior gonopods with a flagella and allowing us to place this specimen in a recent family, the Cambalidae (Enghoff et al. 2015).

Order Spirobolida Bollman, 1893

Family undetermined (9)

New records. 1 F, BuB830; 1 M (head missing), BuB916; 1 M, BuB1795; 1 F, BuB1840; 1?, BuB2616; 1?, BuB3020; 1 M, BuB3000; 1 F, BuB3260; 1 M, ZFMK MYR7373.

Figure 2E

Identification. The tergites, pleurites and sternites are completely fused into body rings. The head has a median suture, a character allowing for these specimens to be distinguished from the 2 other recent orders with complete body rings: Julida and Spirostreptida. A detailed analysis of the male gonopods (Enghoff et al. 2015) is necessary to determine those specimens even to suborder level (e.g. the absence or presence of a tiny sternite connecting the posterior telopods, which are hidden within the anterior telopods), which is beyond the scope of this checklist.

Order Polydesmida Leach, 1815

Family undetermined (161)

New records. 1?, BuB600; 1?, BuB672; 1?, BuB818; 6?, BuB902; 2?, BuB909; 1 M, BuB911; 4?, BuB912; 1?, BuB915; 1?, BuB966; 1 M, BuB975; 1 M, BuB976; 1 M, BuB980; 1 F, BuB983; 1 M, BuB993; 1?, BuB995; 1 M, BuB1029; 1 M, BuB1031-A; 1 M, BuB1035; 1 F, BuB1084; 1 F, BuB1085; 1 M, BuB1146; 1 F, BuB1148; 1 M, BuB1149; 2 M, 5 F, BuB1154; 1 F, BuB1155; 1 F, BuB1156; 1?, BuB1414; 1 F, BuB1548; 1 F, BuB1794; 2 F, BuB1830; 1 F, BuB1832; 1 F, BuB1836; 1 M, BuB1844; 1 M, BuB1847; 1 M, BuB1848; 1 M, BuB1849; 3?, BuB1850; 1 M, BuB1852; 1?, BuB1954A; 3 F, BuB1957; 1?, BuB1958; 2 F, BuB1964; 1?, BuB1967; 1 M, BuB1975; 1 F, BuB1985; 1?, BuB1986; 1 F, BuB1987; 1?, BuB1989B;1?, BuB1992; 1?, BuB1993; 1?, BuB2436; 1?, Bub2437; 1?, BuB2613; 1?, BuB2622; 1?, BuB2624; 1?, BuB2631; 2 F, BuB2632; 1?, BuB2639; 1?, BuB2640; 1?, BuB2645; 1?, BuB2646; 1 F, BuB2647; 1 F, BuB2648; 1?, BuB2653; 1 F, BuB2672; 1 F, BuB2683; 1?, BuB2684; 1?, BuB2686; 1 F, BuB2687; 1 F, BuB2688; 1?, BuB2960; 1?, BuB2967; 1?, BuB2968; 1 F, BuB2969; 1?, BuB2970; 2?, BuB2972; 1 M, BuB2976; 1 F, BuB2982; 2 F, BuB2983; 1?, BuB2987; 1 F, BuB2988; 1 M, BuB2992; 1 M, BuB2994; 1?, BuB2999; 1 F, BuB3001; 1 F, BuB3002; 1 M, BuB3003; 1 F, BuB3004; 1 M, BuB3008; 1?, BuB3011; 1?, BuB3021; 1?, BuB3023; 1 F, BuB3025; 1? BuB3029; 1?, BuB3032; 1 M, BuB3034; 1 M, BuB3039; 1 F, BuB3040; 1 ?, BuB3028; 1 M, BuB3049; 1 M, BuB3055; 1 M, BuB3238; 1 F, BuB3246; 1 F, BuB3251; 1 F, BuB3252; 1 F, BuB3253; 1 F, BuB3254; 1 M, BuB3256; 1?, BuB3265; 2 F, BuB3267; 1?, BuB3269; 1? (posterior half), BuB3270; 1?, BuB3274; 2?; BuB3275; 1?, BuB3276; 1 F, BuB3277; 1?, BuB3278; 1?, BuB3279; 1?, BuB3285; 1 F, BuB3286; 1 M, BuB3293; 1 M, ZFMK MYR06118; 1 F, ZFMK MYR06120; 1 F, ZFMK MYR07374; 1 M, 1?, ZFMK MYR07377; 1 ?, ZFMK MYR07375; 1 M, ZFMK MYR07379; 1 F, Wu F2817/Bu/CJW; 1?, Wu F3385/Bu/CJW; 1?, Wu F3396/Bu/CJW; 1?, Wu F3397/Bu/CJW;

1 F, RO my249; 1 F, RO my301; 1 F, RO my304.

Figure 2F

Identification. These millipedes are flat-backed; the tergites, pleurites and sternites are completely fused into body rings, triangular shaped with extended side wings (paranota). The head is lacking eyes, the tergites are lacking a dorsal suture. The body consists of 18 or 19 rings, the telson carries more or less evident spinnerets (Enghoff et al. 2015). Suborders and families are only determinable after a careful analysis of the male gonopods, which is beyond the scope of this study.

Class CHILOPODA Latreille, 1817

Order Scutigeromorpha Leach, 1814

Family undetermined (7)

Scutigeromorpha spp.

Literature records. 2 ? (Zhang 2017).

New records. 1 ?, BuB63; 1 ?, BuB120; 1 ?, BuB625; 1 ? RO my111; 1 ?, RO my168.

Identification. With 15 legs, all of them long. The stigma openings are located dorsally, and the large eyes consist of numerous ommatidia (Bonato and Zapparoli 2011).

Order Lithobiomorpha Newport, 1844

Family undetermined (2)

New records. 1 ?, RO my340; 1 ?, BuB3289.

Identification. With 15 legs The stigma openings are located laterally, and the eyes consist of few ommatidia (Bonato and Zapparoli 2011).

Order Scolopendromorpha Leach, 1814

Family Cryptopidae Kohlrausch, 1881 (1)

Cryptopidae sp.

Literature record. 1 ? (Zhang 2017).

Family Scolopendridae Leach, 1814 (1)

Scolopendridae sp.

Literature record. 1 ? (Zhang 2017).

Family undetermined (7)

Literature record. 1 ?, NMS G.2010.41.40 (Ross et al. 2010).

New records. 1 ? BuB834; 1 ?, BuB2661; 1 ?, BuB3064; 1 ?, BuB3240; 1 ?, Wu F3395/Bu/CJW; 1 ?, RO my111.

Identification. With 21/23 legs. The stigma openings are located at the pleura, eyes absent or are constisiting of few ommatidia (Bonato and Zapparoli 2011).

Order Geophilomorpha Leach, 1815

Family undetermined (9)

New records. 1 ?, BuB1997; 1 ?, BuB2660; 1 ?, BuB3063; 1 ?, BuB3065; 1 ?, BuB3287; 1 ?, BuB3288; 1 ?, BuB3290; 1 ?, Wu F3402/Bu/CJW; 1 ?, RO my35.

Identification. Legs 30 to more than 100. The stigma openings are pleural, the animals are blind (Bonato and Zapparoli 2011).

Family Geophilidae Leach, 1815 (3)

***Kachinophilus pereirai* Bonato et al., 2014**

Literature records. 1 M, AMNH Bu-Ba41a; 1 ?, AMNH Bu-Ba50a; 1 ?, AMNH Bu-Ba63a.

Class SYMPHYLA Ryder, 1880

Family Scolopendrellidae Bagnall, 1913 (1)

***Symphylella patrickmuelleri* Moritz & Wesener, 2017**

Literature record. 1 ?, ZFMK MYR6269 (Moritz and Wesener 2018).

Family Scutigerellidae Bagnall, 1913 (2)

New records. 1 ?, BuB3292; 1 ?, BuBXY.

Identification. The antennae are consisting of more than 20 articles, the scuta of the tergites are well-rounded, the leg bases carry styli (see Moritz and Wesener 2018).

Corrections of misidentifications by Zhang (2017)

Zhang (2017), in his large book about inclusions in amber, listed numerous interesting arthropod specimens, rivaling most public museum collections in the diversity of the presented inclusions. He also listed several myriapod specimens with impressive preservation quality. Unfortunately, many of the records were determined to the level of a Recent genus, and some of these identifications are clearly wrong, which we correct below:

Chilopoda, Lithobiomorpha

"Lithobiomorpha sp." (Zhang 2017: 132–133) = Chilopoda sp. This is clearly a juvenile that cannot be determined.

Polyxenidae

The mentioned specimens can only be determined to genus level based on detailed head characteristics that cannot be examined from the photographs. Therefore, the figured specimens only show characters of the family, not of any specific genus.

"*Unixenus* sp." (Zhang 2017: 144) = Polyxenidae sp. The figure shows a polyxenid. Diagnostic characters of the genus *Unixenus* are not visible.

"*Propolyxenus* sp." (Zhang 2017: 144) = Polyxenidae sp. The figure shows a polyxenid. Diagnostic characters of the genus *Propolyxenus* are not visible.

"*Polyxenus* sp." (Zhang 2017: 145) = Polyxenidae sp. The figure shows a polyxenid. Diagnostic characters of the genus *Polyxenus* are not visible. In fact, the single tuft of caudal setae is more of an indication of *Unixenus*.

Order Glomerida

The pictured specimens are clearly Polyzoniida.

"*Glomeridella* sp." (Zhang 2017: 150–151) = Polyzoniida sp. The figured specimen is clearly not a member of *Glomeridella*, a European genus of dwarf pill millipedes (Enghoff et al. 2015, Oeyen and Wesener 2018).

Order Sphaerotheriida

The specimens figured by Zhang (2017) are quite interesting, as there is no fossil record of the order Sphaerotheriida yet (Wesener and VandenSpiegel 2009, Wesener et al. 2010, Wesener 2016) and we also did not recover any specimens in the vast amount of material studied by us.

"Zephroniidae sp." (Zhang 2017: 154–155) = Glomerida. The figures clearly show Glomerida, as visible on the exposed head in 1 of the specimens and the striae at the thoracic shield.

Order Platydesmida

This order also is unknown as fossils. Unfortunately, the alleged specimens figured by Zhang (2017) belong to other orders.

"*Brachycybe* sp. 1" = Siphonophorida. The head morphology and the absence of a dorsal suture clearly identify the pictured specimen as a member of the Siphonophorida and not a Platydesmida (Blanke and Wesener 2014, Enghoff et al. 2015).

"*Brachycybe* sp. 2" = undetermined. This specimen lacks a distinct dorsal suture, and can therefore not be a Platydesmida (Blanke and Wesener 2014, Enghoff et al. 2015). The head is missing, which makes a clear identification impossible, but this specimen otherwise shows characters observed in species of the Siphonophorida.

Order Polyzoniida

"*Bdellozonium* sp." (Zhang 2017: 182–183) = Siphonotidae sp. This specimen was determined to the wrong family. The telson, head and legs clearly show that this is a member of the Siphonotidae, not Polyzoniidae. We are unsure how Zhang determined this specimen to the genus *Bdellozonium*, a recent genus with 2 species in California (Enghoff et al. 2015), which are much larger and can only be determined by a study of the gonopods, which are absent in the pictured specimen.

Order Siphonophorida

Here, 1 of the 5 specimens is determined to the wrong order, while the other 4 are in the wrong family. Nevertheless, Zhang's record confirms our observation that this order is frequently found in Burmese amber.

"Siphonorhinidae sp. 2" (Zhang 2017: 167), "Siphonorhinidae sp. 3" (Zhang 2017: 168), "Siphonorhinidae sp. 4" (Zhang 2017: 168), "Siphonorhinidae sp. 5" (Zhang 2017: 169), all = Siphonophoridae. All these Siphonophorida are members of the family Siphonophoridae, which can be easily distinguished from Siphonorhinidae (also not uncommon in Burmese amber, see above) based on the shape of the head and antennae characteristics (Enghoff et al. 2015). Species of Siphonophoridae are very difficult to determine to the genus or even species because the taxonomy is chaotic (Jeekel 2001, Read and Enghoff 2009). Careful descriptions of the tiny gonopods are a necessity in order to not create more chaos.

Order Chordeumatida

Unfortunately, all alleged specimens are members of the order Polydesmida, not Chordeumatida as is evident from the body-ring number and the absence of ommatidia. Chordeumatida sometimes lack ommatidia, mainly in cave taxa (Liu et al. 2017b). We do not know how Zhang could determine the exclusively female specimens to family, or even genus, as a careful observation of the male gonopods would have been necessary.

Anthroleucosomatidae sp. (Zhang 2017: 176) = Polydesmida.

"*Tingupa* sp. 1" (Zhang 2017: 176) = Polydesmida.

"*Tingupa* sp. 2" (Zhang 2017: 177) = undetermined, possibly Polydesmida or Platydesmida.

Order Spirostreptida

"*Cambala* sp." (Zhang 2017: 172) = Cambalidea. Even most families of the Spirostreptida, and especially those belonging to the suborder Cambalidea, can only be determined after a careful examination of the gonopods (Enghoff et al. 2015). The figured specimen is female, so it cannot be determined below the level of suborder.

Order Polydesmida

"Paradoxosomatinae sp." (Zhang 2017: 179–180) = Polydesmida. Families and subfamilies of Cretaceous Polydesmida can only be determined after a careful observation of the male gonopods. Unfortunately, the gonopods are not visible in the specimen, and therefore, it might be any Polydesmida. Elongated legs are often found in Recent species of the family Paradoxosomatidae, but it is entirely possible that 100 mya other families of Polydesmida had species with elongated legs.

"*Scytonotus* sp." (Zhang 2017: 180) = Polydesmida. *Scytonotus* is a genus of Polydesmida currently endemic to North America. Species can only be assigned to this genus based on gonopod characteristics. Families and subfamilies of Cretaceous Polydesmida can only be determined after a careful observation of the male gonopods. Unfortunately, the gonopods are not visible in the specimen, and therefore, it might be any Polydesmida.

Abundance of Myriapoda in Burmese amber

In the studied Burmese amber, 13 of the 16 extant orders of millipedes are represented. Only the orders Sphaerotheriida, Julida and Siphonocryptida are missing. In the studied collections, the Colobognatha are dominant, although several specimens (15–20) could not be determined to order level and are therefore not included in our list. Among the specimens determined to order, the Polydesmida are dominant with 30.55% of all recorded fossils. The abundances of the remaining orders are as follows: Polyxenida = 15.37%, Glomeridesmida =

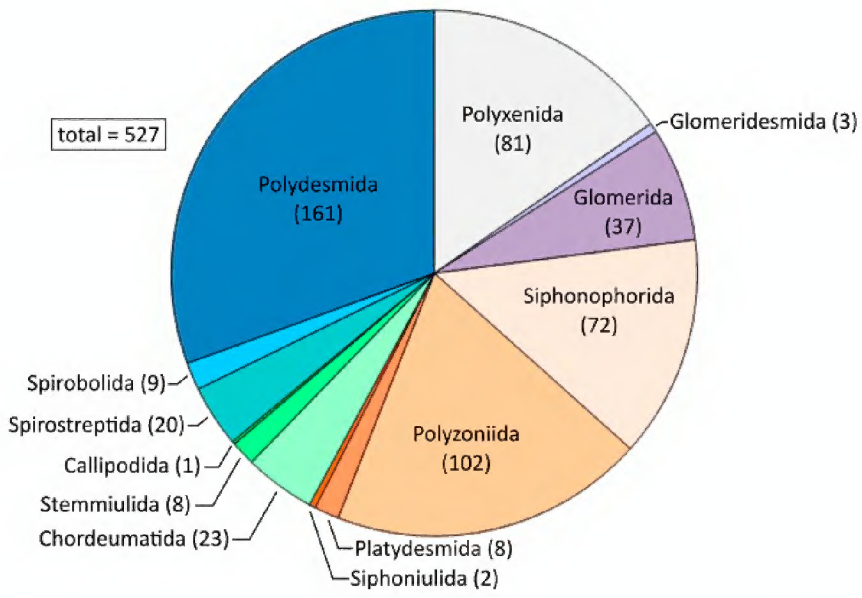

Figure 3. Relative abundance of millipede orders preserved in the studied Cretaceous Burmese amber and reported in the literature. In total 527 millipedes are listed in this publication and the literature. The orders Sphaerotheriida, Julida and Siphonocryptida are not known from Burmese amber.

0.57%, Glomerida = 7.02%, Siphonophorida = 13.66%, Polyzoniida = 19.36%; Platydesmida = 1.52%, Siphoniulida = 0.38%, Chordeumatida = 4.36%, Stemmiulida = 1.52%, Callipodida 0.19%, Spirostreptida = 3.8%, and Spirobolida = 1.71% (Fig. 3). In centipedes, 4 of the 5 extant orders are present in the studied Burmese amber.

Discussion

Present knowledge of the Myriapoda of Myanmar is quite limited. Most records are more than 120 years old and a Recent species list of the Diplopoda lists only 8 orders: Glomerida, Sphaerotheriida, Siphonophorida, Chordeumatida, Polydesmida, Julida, Spirostreptida, and Spirobolida (Likhitrakarn et al. 2017), of which 6, all but Sphaerotheriida and Julida, are also recorded from Cretaceous amber. Species of 7 orders, Polyxenida, Glomeridesmida, Polyzoniida, Platydesmida, Siphoniulida, Stemmiulida and Callipodida, are present in the Cretaceous fauna, but they have no records yet from Myanmar. However, given the known worldwide distribution of the groups (Shelley and Golovatch 2011), all 7 of those millipede groups can be expected from Myanmar once extensive faunal inventories are conducted.

Burmese amber contains the oldest fossils and/or first fossils for 9 of the 16 orders of Diplopoda: Polyxenida, Glomerida (Fig. 1A), Glomeridesmida (Fig. 1B), Siphonophorida (Fig. 1C), Polyzoniida (Fig. 1D), Platydesmida (Fig. 1E), Chordeumatida (Fig. 2A), Stemmiulida (Fig. 2B) and Spirostreptida (Fig. 2D). At the family level, the oldest/first fossils of 9 representatives are known from Burmese amber: Synxenidae and Polyxenidae (both Polyxenida), Glomeridesmidae, Siphonophoridae, Siphonorhinidae, Siphonotidae, Siphoniulidae, Heterochordeumatidae and Cambalidae. The minimum age of these order- and family-level taxa is therefore 99 mya. As shown by Shelley and Golovatch (2011), these orders most likely evolved long before the Cretaceous, based on the fossil record and biogeographic data.

For Chilopoda, the 4 orders represented in the fossil records, Scutigeromorpha, Lithobiomorpha, Scolopendromorpha and Geophilomorpha, have a worldwide distribution and several recent species occur in Myanmar. Here, family determinations, which are beyond the scope of this checklist, might provide more input on potential faunal change that occurred since the Cretaceous in Southeast Asia.

The high abundance of Polyzoniida and the presence of polyzoniid juveniles with as few as 4 leg pairs indicates a strong sampling bias towards this group, of which 1 or several species probably lived and reproduced on the amber-producing trees.

With this list the Cretaceous Diplopoda fauna of Myanmar is now better known than the Recent one, which is an indication of the need of more inventories and taxonomic studies on the fauna of this megadiverse country. This first checklist of the millipede fauna preserved in Cretaceous Burmese amber will serve as a starting point for further research. More detailed descriptions of families, genera and species, based on the reconstruction of the gonopods and telopods, will unfortunately take years to accomplish.

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Authors' Contributions

TW and LM sorted and determined the studied specimens. TW wrote the text.

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